

ECOLOGICAL CHARACTERISTICS AND DISTRIBUTION OF *ARBUTUS XALAPENSIS* (TEXAS MADRONE) POPULATIONS IN CENTRAL TEXAS

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ABSTRACT

Arbutus xalapensis Kunth (Texas madrone, Ericaceae) is found in western and central Texas, but its ecological characteristics are little known. Mature *A. xalapensis* plants were found in the Albert and Bessie Kronkosky State Natural Area in Kendall and Bandera counties, central Texas (29.740278 N, –98.838333 W). Habitats studied included *Acer grandidentatum* Nutt. (bigtooth maple) canyon bottoms, *Juniperus ashei* J.Buchholz/*Quercus* L. sp. (Ashe juniper/mixed oak) hillsides, and *J. ashei* uplands. Population characteristics were compared to habitat and surface geology. A total of 98 *A. xalapensis* plants were found in the communities studied. Differences were found for all parameters except height. Upland *A. xalapensis* trees had the lowest mean ($\pm$ SD) density (2 ± 3 plants/ha), highest basal area (210 ± 190 cm²/plant), community elevation (573 ± 14 m) and height (4.09 ± 1.70 m/plant). Hillside communities had the highest density (61 ± 38 plants/ha), but lower basal area (110 ± 170 cm²/plant). The canyon bottom plant basal area was 80 ± 100 cm²/plant and density was 10 ± 5 plants/ha. The canyon bottoms had the deepest soil (27.2 ± 20.4 cm) and lowest elevation (510 ± 16 m). When geological substrates were examined, 128 additional plants were found. The largest plants were on the Fort Terrett member of the Edwards limestone (hard limestone, 230 ± 220 cm²/plant), but density was the lowest (2 ± 3 plants/ha). Whereas greater density was on the Upper Glen Rose limestone (softer limestone, 16 ± 7 plants/ha), where plants were smaller (110 ± 150 cm²/plant). Community type and geological substrate seem critical for growth of this species.

Key Words: basal area, Edwards's limestone, Glen Rose Limestone, habitat preference, *Juniperus* woodland, juniper/oak woodland, limestone soil, plant density.

Species establish in particular habitats based on the biotic and abiotic characteristics of the habitat and the specific needs or requirements of the species (Morin 2011; Keddy 2017). Showing the exact location where a specific plant, species, or community occurs is relatively easy to do, but determining the niche and requirements for an individual species is very difficult (Keddy 2017). Understanding community necessities is even more difficult due to the large number of species and the multitude of requirements. Studying a single species within a larger community can help one understand how the whole community functions (Joshi and Joshi 2009; Keddy 2017).

Arbutus xalapensis Kunth (Texas madrone, Ericaceae) appears to have a disjunct distribution in Texas, found on the Balcones Escarpment in the southeastern and south-central Edwards Plateau and in the mountains of the Trans – Pecos region of west Texas (Fig. 1). In earlier quantitative plant ecological studies in central Texas *Arbutus xalapensis* was not detected in transects where plant communities were measured (Van Auken et al. 2017). However, it was sighted in the area in a number of places (Van Auken, personal observation). Its density was so low it was not found in any of the quadrats sampled or in any of the communities surveyed. Based on the size of the sample, at least one-half hectare would have to be completely examined before *A. xalapensis* would be encountered. This species is not listed as an

endangered or threatened species (Poole et al. 2007), but it is fairly rare in central Texas. There seem to be some specific conditions required for the presence and growth of this species, but at this point, they are not known.

Estimating abundance or density and other aspects of a rare or elusive species is difficult to do (Thompson 2004). These are species that have low density, a restricted distribution, or a low probability of detection. Usually, a rare plant study will define a geographic area containing the species of interest to study and then partition the area into sampling units, such as communities or habitats, then subsequently divide it into plots, transects, and /or quadrats (Thompson 2004). Thus, the procedure seems to be a two-step process requiring a two stage sampling design. Therefore, the selection of sampling units or habitats is the first stage and the counting or measuring of individuals is the second stage (Thompson 2004).

Arbutus xalapensis is found in western as well as central Texas, but its ecological characteristics are not well known. It is one of at least 12 species of *Arbutus* worldwide (Gonzalez-Elizondo et al. 2012; USDA 2016). It is an evergreen tree, typically 4–6 m tall, but can be up to 15 m tall (Sorensen 1995; Mackay 1996) with a trunk circumference up to 2.5 m under favorable conditions (Tirmenstein 1990, Fig. 2). In the United States, *A. xalapensis* occurs in Texas and New Mexico, but its distribution continues

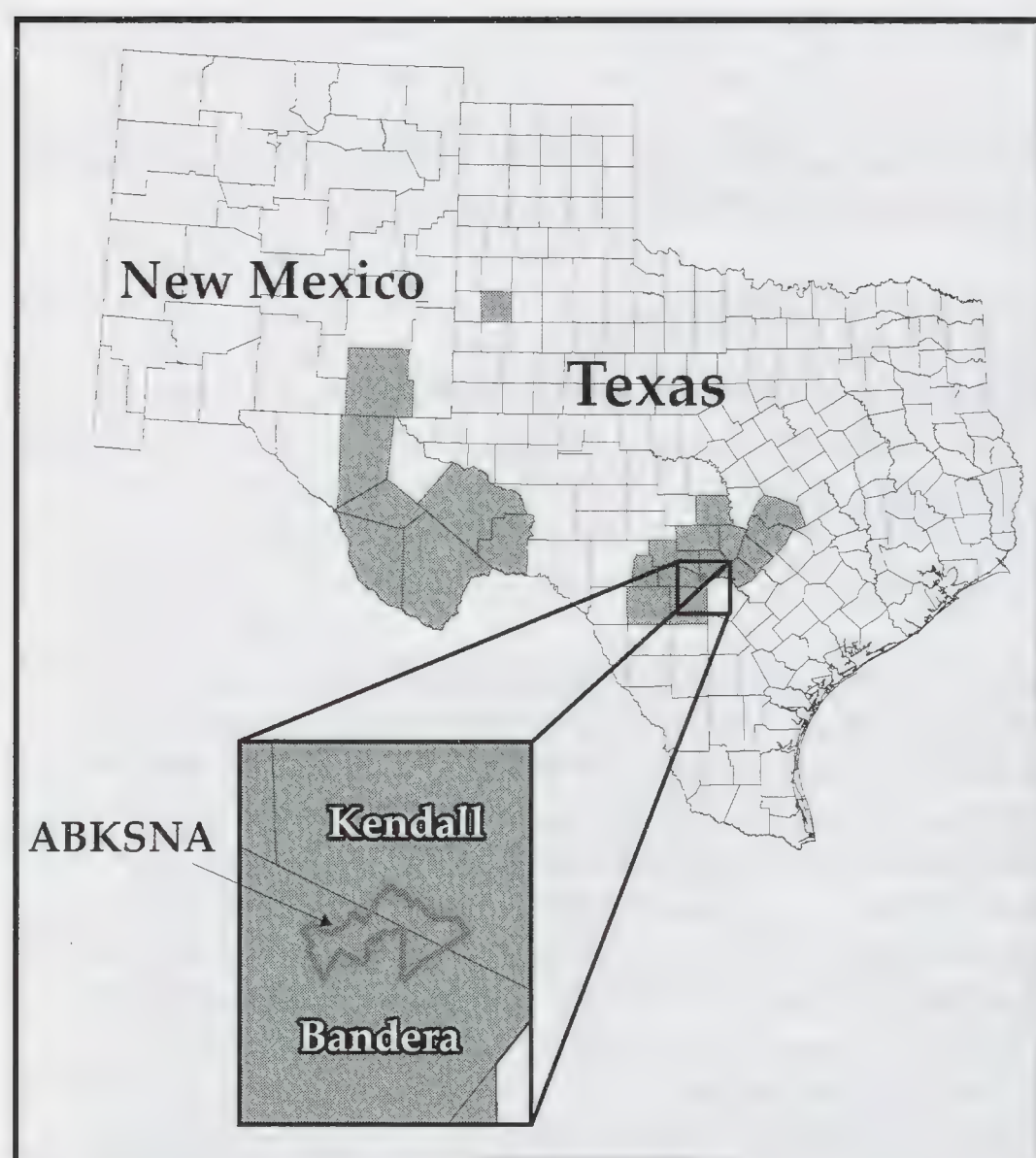


FIG. 1. Map of New Mexico and Texas showing county outlines and shaded counties having *Arbutus xalapensis* plants. The blowup shows most of Kendall and Bandera counties with the outline and arrow showing the Albert and Bessie Kronkosky State Natural Area where the study was carried out (approximately 29.740278 N, -98.838333 W).

southward at higher elevations through most of Mexico, as well as in Guatemala, Honduras, El Salvador, and Nicaragua (Sorensen 1995). In southern Mexico, its elevation ranges from 1500–3400 m in forests with canopy heights of 25–33 m (Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). *Arbutus xalapensis* is found on the Balcones Escarpment in the southeastern and south-central Edwards Plateau and in the mountains of the Trans-Pecos region of west Texas at elevations of about 1219–2286 m (Tirmenstein 1990). This elevation suggests plants are above the Chihuahuan desert communities, probably on hillsides above the desert.

Arbutus xalapensis is reported growing in wooded canyons, western slopes, and dry creek beds (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). It is reported in riparian woodlands with *Populus deltoides* W.Bartram ex Marshall (Eastern cottonwood), *Salix exigua* Nutt. (coyote willow), *Quercus grisea* Liebm. (gray oak), and *Acer grandidentatum* Nutt. (bigtooth maple) (Tirmenstein 1990). Thus, *Arbutus xalapensis* has been documented in a variety of communities containing multiple species of *Quercus* L. (oak), *Juniperus* L. (juniper), *Pinus* L. (pine), and *Ulmus crassifolia* Nutt. (cedar elm) (Tirmenstein 1990). Consequently, its specific habitat seems uncertain and habitat requirements are not known. Much of what is reported for *A. xalapensis* seems to consist of anecdotal or general observations.

In the Edwards Plateau region of Texas, *J. ashei* has been reported to serve as a nurse tree for juvenile *A. xalapensis* plants (Tirmenstein 1990), and juveniles are rarely present beneath mature *A. xalapensis* trees (Van Auken personal observation; also described in Whitenberg and Hardesty 1978). *Juniperus* mulch may increase the soil water-holding capacity, allowing more successful *A. xalapensis* establishment and/or *J. ashei* trees or thickets may protect the juveniles from herbivory (Tirmenstein 1990; Van Auken, personal observation). Light intensity and water availability have been shown to have significant impacts on seedling development (Whitenberg and Hardesty 1978). Seedlings of some other species can germinate in shade and then grow slowly for more than 35 years, but seem to require full sun to mature (Van Auken et al. 2004; Kane et al. 2011). The same may be true for *A. xalapensis* plants, but this is unknown at present.

The purpose of this study was to examine some of the ecological characteristics of populations of *Arbutus xalapensis* in central Texas. This project seeks to identify various biotic and abiotic factors that may influence the growth and distribution of *A. xalapensis* populations across the landscape in the Edwards Plateau region of Texas.

METHODS

Study Site

This study was carried out within the southeastern portion of the Edwards Plateau ecological region of Texas (approximately 29.740278 N, -98.838333 W), referred to as the Balcones Canyonlands (Fig.1). The Balcones Canyonlands are characterized by dry to mesic slopes supporting *Juniperus ashei* - *Quercus fusiformis* Small (live oak) - *Diospyros texana* Scheele (Texas persimmon) woodlands and *Taxodium distichum* Kunth. (bald cypress) - *Carya illinoensis* (Wagninh.) K.Koch (pecan) - *Celtis laevigata* (Kunth.) Spreng. (hackberry) - *D. texana* riparian communities (Riskind and Diamond 1988). The study site is located within the eastern portion of the Edwards Plateau, which has a mean annual precipitation of about 85 cm/yr, with considerable variation and almost no rainfall in June, July, and August (Riskind and Diamond 1988; Van Auken and Ford 2017). In addition, steep walled canyons and some north facing slopes support limited deciduous communities (Van Auken 2018). The east-central Edwards Plateau average summer high temperature is 35°C and the average winter low temperature is 4°C (Riskind and Diamond 1988).

The specific research study site is located within the Albert and Bessie Kronkosky State Natural Area (ABKSNA) within portions of both Bandera and Kendall counties, TX, and is approximately 1520 hectares (3757 acres), and is high-fenced (Fig.1). The study area ranges in elevation from approximately

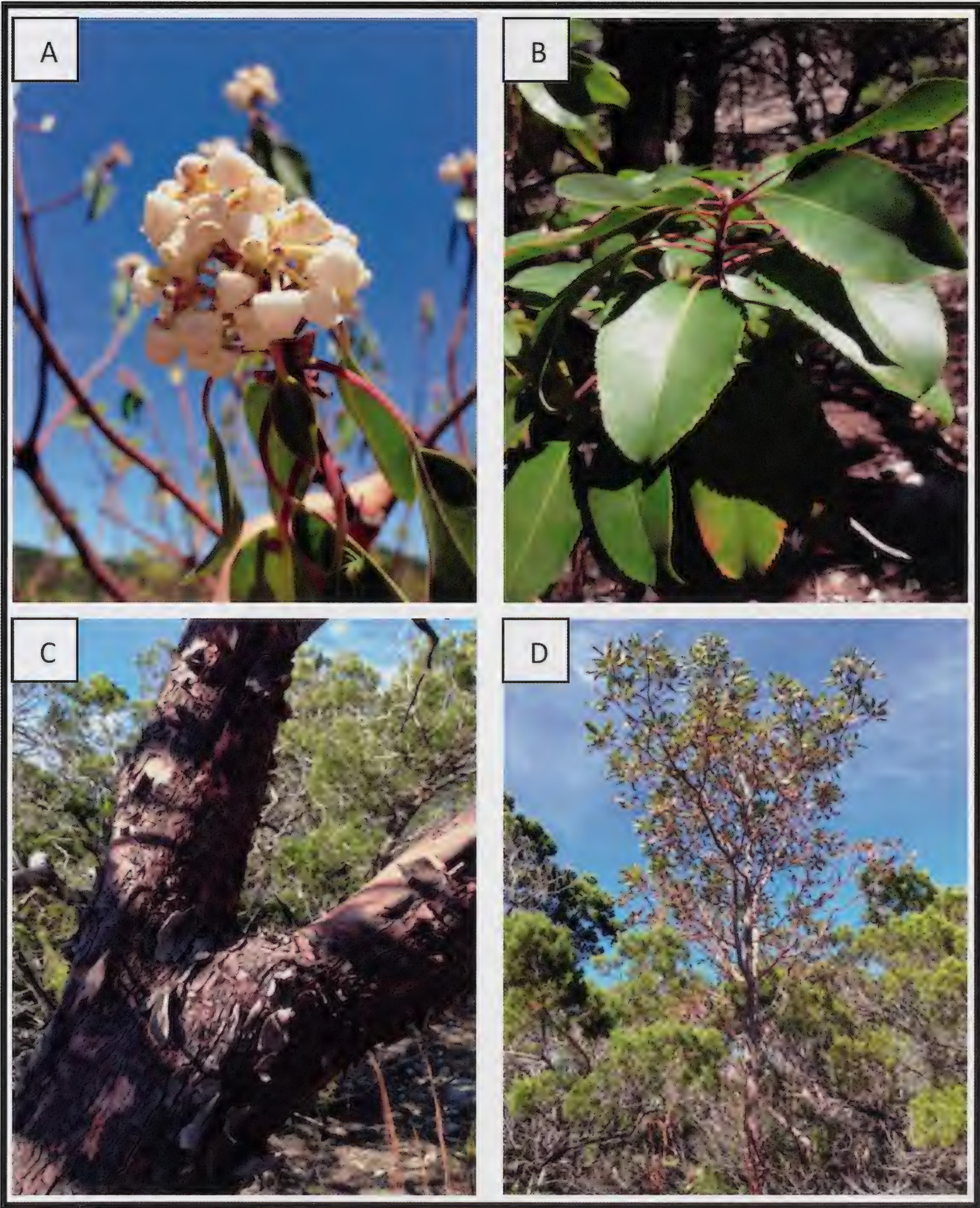


FIG. 2. General pictures of *Arbutus xalapensis* taken at the study site showing notable traits. (A) *Arbutus xalapensis* inflorescence, (B) *A. xalapensis* leaves, (C) *A. xalapensis* bark exfoliation, and (D) mature *A. xalapensis* tree at the Albert and Bessie Kronkosky State Natural Area.

481–614 m above mean sea level (Van Auken et al. 2017). Geologic formations present at the site include the Fort Terrett Member of the Edwards Limestone formation in the upper elevations and Upper Glen Rose limestone formation below the Edwards with

relatively deep calcareous silty clay soil (Mollisols over limestone bedrock, USDA NRCS 2016). In the canyon bottoms at lower elevations the soils are deeper and mostly overlay Upper Glen Rose limestone (USGS - TWDB 1976).

Sampling Methods

Vegetation surveys were carried out in the “Tin Cup Canyon” and associated areas in the north-eastern portions of the ABKSNA (Van Auken et al. 2017). Despite their close proximity (< 0.25 km), the upland and canyon communities differ in many respects. The upland communities were relatively flat with shallow soils, while the canyon communities had greater slopes and deeper soils. Van Auken et al. (2017) found less dense canopy cover within the upland juniper canopies than beneath maple canopies in canyons, however, the understory in the uplands were more densely vegetated than canyon understory communities. Dominant canyon species were found to be *Acer grandidentatum*, *J. ashei*, *Prunus serotina* Poit. and Turpin, and *Quercus laceyi* Small. While the dominant upland species were *J. ashei* and *Sophora secundiflora* (Ortega) Lag. ex DC. However, no *A. xalapensis* juveniles or trees were reported (Van Auken et al. 2017).

Three distinct habitats were chosen for this study: canyons bottoms, hillsides, and uplands. Each habitat was surveyed specifically for *A. xalapensis*. Surveys consisted of arbitrarily walking through the various habitats until an *A. xalapensis* individual was found and then measuring basal diameter (cm), height (m), and soil depth (cm), as well as collecting GPS coordinates and elevation, then resuming the search for additional *A. xalapensis* plants. This process was replicated in each habitat type in the Tin Cup Canyon area. To account for non-uniformity in basal diameter, 80 cm tree calipers were used to measure basal diameter at a minimum of two points per tree. These measurements were taken at ground level and then averaged (Van Auken et al. 1981; Bush and Van Auken 2015). Height was measured using a marked pole (Powell 2005; Bush and Van Auken 2015). Between two and four soil depth measurements, on opposite sides of *A. xalapensis* trees were made by hammering 60 cm long rebar into soil until reaching bedrock (Larcher 2003). After reaching the bedrock, the rebar was removed and soil penetration (depth) was measured on the rebar using a measuring tape (Van Auken et al. 1981).

Due to low density, *A. xalapensis* plants were difficult to locate. Previous uses of the quadrat procedure did not include any *A. xalapensis* individuals in an earlier study despite density stabilization curves indicating adequate sampling (Van Auken et al. 2017). Thus, a distance technique was used to sample these populations (Cottam and Curtis 1956). The nearest neighbor method was used, but only *A. xalapensis* individuals were measured (Cottam and Curtis 1956; Barbour et al. 1987). Mature trees were included if their basal diameters were greater than 1 cm and were greater than 1.56 m in height (Bush and Van Auken 2015). Coordinates of each mature *A. xalapensis* tree

located were uploaded into ArcMap (Version 10.3, ESRI, Inc., Redlands, CA) and distances between mature *A. xalapensis* trees were later determined. The nearest neighbor was restricted to the nearest mature *A. xalapensis* tree found within an 180° area of inclusion from the base of the first tree found and at a perpendicular to the direction of travel (Cottam and Curtis 1956; Barbour et al. 1987). The distance from one individual *A. xalapensis* tree to its nearest neighbor of the same species was found using GPS coordinates (Cottam and Curtis 1956; Barbour et al. 1987; Kane and Ryan 1998). GPS coordinates were also used to measure elevation above mean sea level. The mean distance between neighbors across all plants encountered in each community was determined and *A. xalapensis* density was calculated as follows: $\text{total density} = 10,000\text{m}^2 / (2 * \text{mean distance}^2)$ (Barbour et al. 1987). Density stabilization curves showed stable density or sampling adequacy in all habitats examined (Davis and Van Auken, unpublished data).

Geologic Survey

To determine the importance of the underlying geology to the density of *A. xalapensis*, data from another area were collected and analyzed using a geologic map in ArcMap (USGS - TWDB 2007). All data collection techniques were consistent with those previously described. Transects were carried out on the Fort Terrett Member of the Edwards limestone and Upper Glen Rose Formation. Measurements included density, basal area, height, and soil depth. Sample size was 128 *A. xalapensis* plants.

Statistical Analysis

To show differences among habitat types, JMP statistical software was used (Version 12, SAS Institute, Cary, NC; Sall et al. 2012). Initially, data were organized by habitat groupings (canyon, hillside, and upland), and then analyzed. Summary statistics (means and standard deviations) were calculated for each habitat type and each data set was tested for normality using the Shapiro-Wilk test. Shapiro-Wilk tests resulted in non-normally distributed data. Due to differences in sample sizes and high variance, as well as non-normally distributed data, non-parametric statistics were utilized. Kruskal-Wallis tests were completed to determine if the density, height, elevation, basal area, and soil depth parameters were different between habitat types ($\alpha = 0.05$) (Sall et al. 2012). Dunn's post hoc test was used to show where significant differences occurred (Dinno 2015). The non-parametric Mann-Whitney U tests were used to show significant differences in the parameters listed above between communities on Fort Terrett and Glen Rose geological substrates ($\alpha = 0.05$) (Sall et al. 2012).

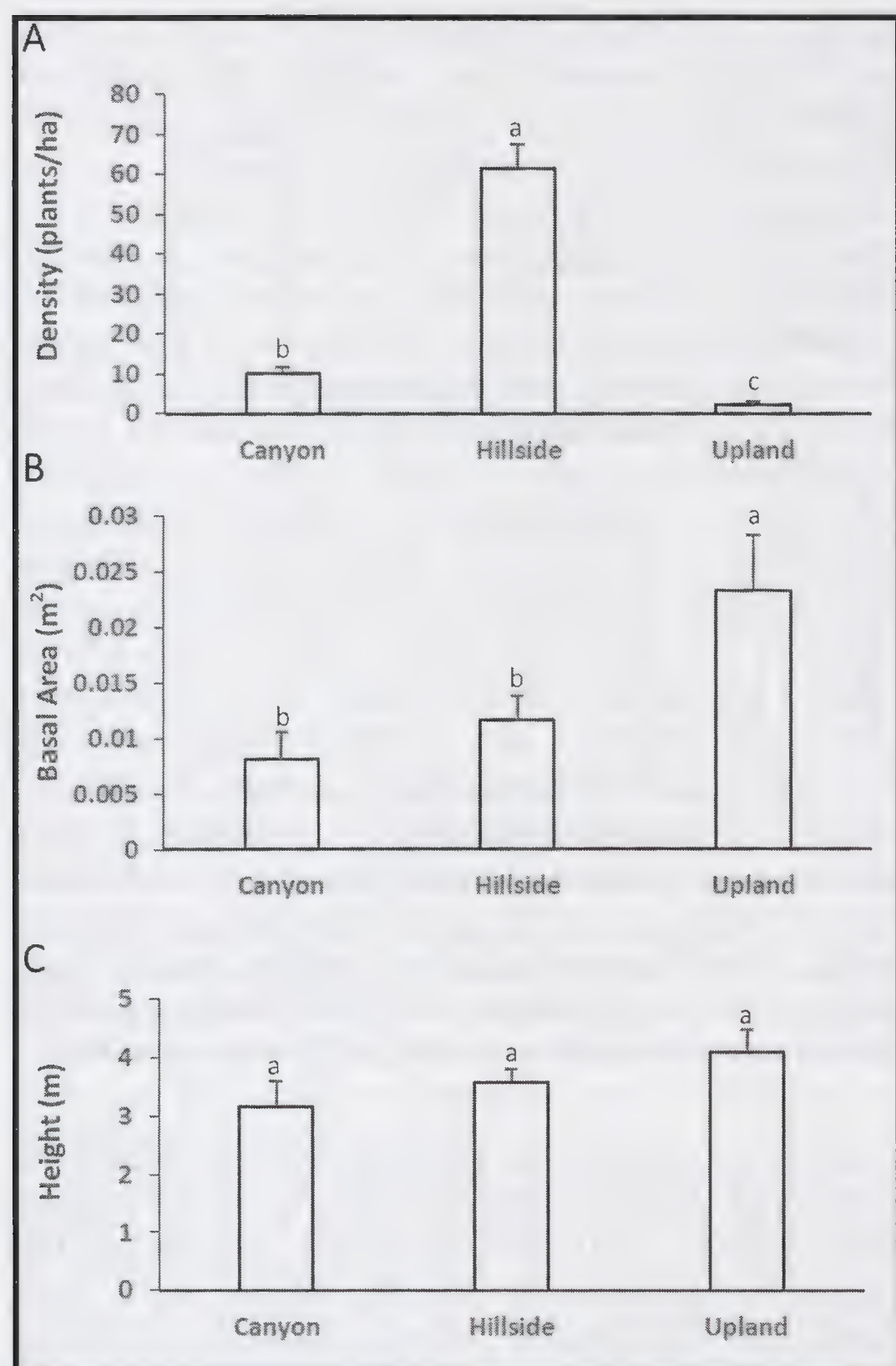


FIG. 3. Comparisons of mean (± 1 SD) *Arbutus xalapensis* traits by habitat type. (A) density, (B) basal area, and (C) tree height. Sample size was 98 plants. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

RESULTS

Community Comparisons

There was a significant difference in *A. xalapensis* density among the three communities studied (Kruskal–Wallis Test, $\chi^2 = 58.38$, $df = 2$, $P < 0.001$, Fig. 3A). Dunn's post hoc test revealed differences between canyon and hillside communities ($Z = -4.904$, $P < 0.001$), canyon and upland communities ($Z = 2.026$, $P = 0.043$), and hillside and upland communities ($Z = 7.564$, $P < 0.001$) (Fig. 3A). Mean density ($\pm$ SD) was 10 ± 5 plants/ha in the canyon bottoms, 61 ± 38 plants/ha in the hillside and 2 ± 3 plants/ha in the upland or hill top communities.

A significant difference was also found in basal area among the three communities (Kruskal–Wallis Test, $\chi^2 = 10.19$, $df = 2$, $P = 0.006$, Fig. 3B). Dunn's post hoc test showed differences between the canyon and upland communities ($Z = -2.928$, $P = 0.003$), as well as between hillside and upland communities ($Z = -2.818$, $P = 0.005$), but not between canyon and hillside communities ($Z = -0.828$, $P = 0.408$) (Fig.

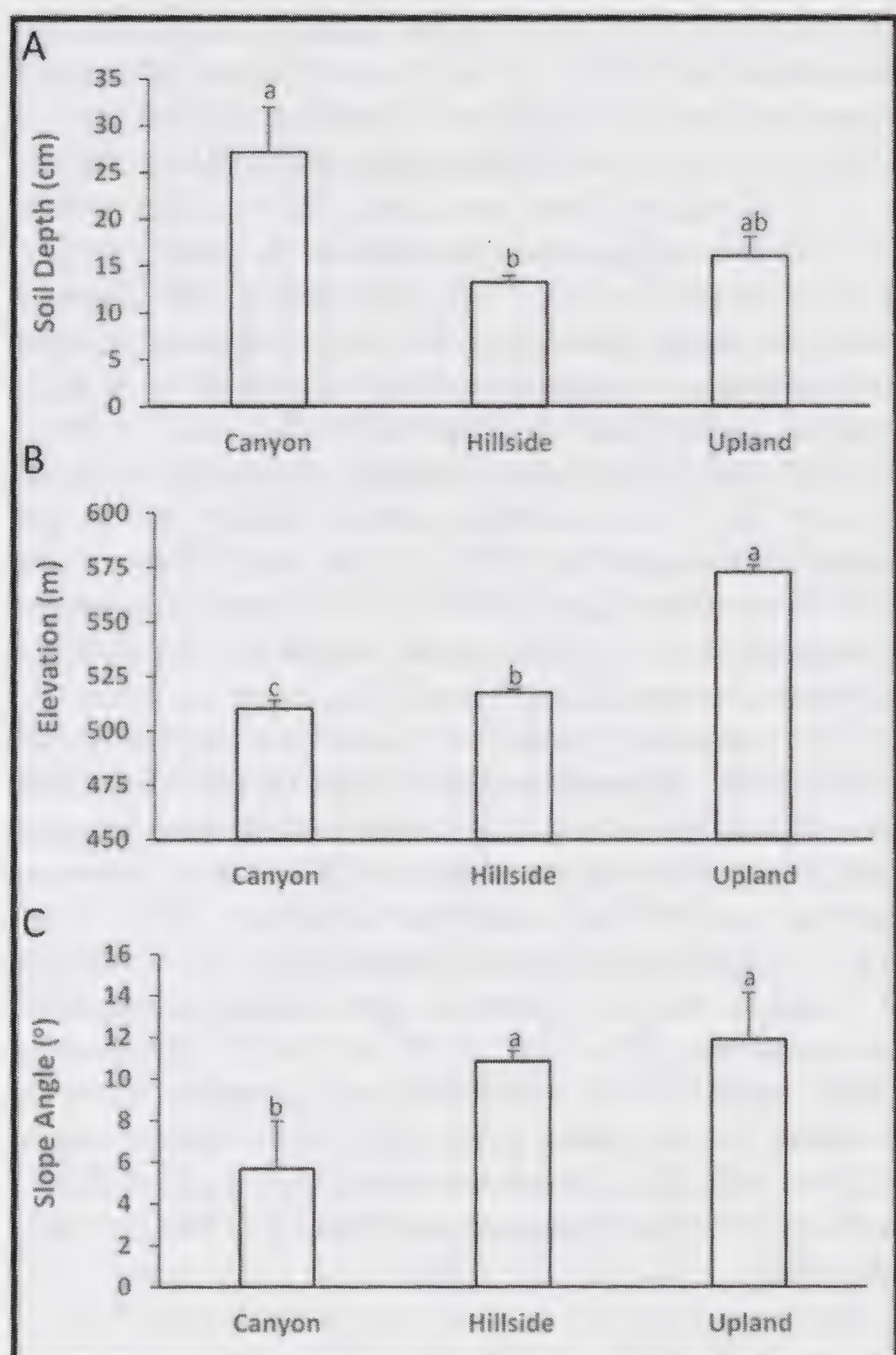


FIG. 4. Comparison of mean (± 1 SD) *Arbutus xalapensis* sites by habitat type. (A) soil depth, (B) habitat type, and (C) slope angle. Sample size was 98 plants. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

3B). Greatest *A. xalapensis* basal area was in the hilltop communities at 210 ± 190 cm/plant, followed by the hillside at 110 ± 170 cm/plant and canyon bottom communities at 80 ± 100 cm/plant. The data suggest an overall trend of increasing basal area from the canyon bottom communities to the upland communities (Fig. 3B).

Plant height did not significantly differ among the three communities studied (Kruskal–Wallis Test, $\chi^2 = 3.82$, $df = 2$, $P = 0.148$). Though no statistical differences were found, a trend of increasing height can be seen with shortest plants occurring within canyon bottom communities (3.2 ± 1.8 m) and the tallest (4.1 ± 1.7 m) occurring within upland communities (Fig. 3C).

A marginally significant difference in soil depth was found among the three *A. xalapensis* communities (Kruskal–Wallis Test, $\chi^2 = 5.96$, $df = 2$, $P = 0.051$) (Fig. 4A). Dunn's post hoc test showed a statistically significant difference between the canyon and hillside communities ($Z = 2.261$, $P = 0.024$), but not between canyon and upland communities ($Z = 0.686$, $P = 0.493$) or hillside and upland communities

($Z = -1.407$, $P = 0.159$). Canyon communities had the deepest soil (27.2 ± 2.1 cm), followed by upland communities (16.0 ± 8.6 cm) with the shallowest soil (13.3 ± 5.5 cm) in hillside communities (Fig. 4A).

For elevation there was a significant difference in the three *A. xalapensis* communities (Kruskal–Wallis Test, $\chi^2 = 49.39$, $df = 2$, $P = 0.010$) (Fig. 4B). Dunn's post hoc test revealed differences between canyon and hillside communities ($Z = -2.546$, $P = 0.011$), canyon and upland communities ($Z = -6.711$, $P < 0.001$), and hillside and upland communities ($Z = -5.810$, $P < 0.001$). The highest elevation was in the upland communities (573 ± 14 m) followed by hillside communities (518 ± 14 m) and the lowest elevation (510 ± 16 m) was found within canyon bottom communities (Fig. 4B).

There was a significant difference in slope angle in the three *A. xalapensis* communities (Kruskal–Wallis Test, $\chi^2 = 12.12$, $df = 2$, $P < 0.005$) (Fig. 4C). Dunn's post hoc test demonstrated differences between canyon and hillside communities ($Z = -3.367$, $P < 0.01$), canyon and upland communities ($Z = -2.789$, $P < 0.01$), but not between the hillside and upland communities ($Z = -0.112$, $P < 0.05$). The lowest slope angle ($5.59^\circ \pm 2.28^\circ$) was found in canyon bottom communities (Fig. 4C). The highest slope angle was in the upland communities ($11.89^\circ \pm 2.26^\circ$) followed by the hillside communities ($10.84^\circ \pm 0.51^\circ$) (Fig. 4C).

Geological Comparisons

The mean basal area ($\pm$ SD) of *A. xalapensis* was significantly higher on the Fort Terrett member substrates, 230 ± 220 cm²/plant, compared to the Upper Glen Rose Formation substrates, 110 ± 150 cm²/plant (Mann-Whitney U-Test, $W = 632.5$, $P = 0.029$, $n = 128$) (Fig. 5A). Significant differences were found between the geology substrates regarding density of *A. xalapensis*. The Fort Terrett member of the Edwards limestone had an *A. xalapensis* density of 2 ± 3 plants/ha and plants on the Upper Glen Rose had a density of 16 ± 7 plants/ha ($W = 1702.5$, $P < 0.001$, $n = 128$) (Fig. 5B). Mean height was higher among Fort Terrett member of the Edwards limestone sites, 3.93 ± 1.82 m, compared to Upper Glen Rose sites, 3.41 ± 1.57 m, but not significantly different ($W = 792$, $P = 0.289$, $n = 128$). Elevation was higher on Fort Terrett sites, 574.63 ± 12.69 m, compared to Upper Glen Rose sites, 515.71 ± 13.01 m ($W = 640$, $P = 0.031$, $n = 128$). Mean soil depth was deeper in Upper Glen Rose sites compared to Fort Terrett member of the Edwards limestone sites (15.32 ± 11.17 cm and 14.09 ± 4.42 cm, respectively) but not significantly different ($W = 814.5$, $P = 0.367$, $n = 128$).

DISCUSSION

Juniperus-Quercus woodlands are a major component of the Edwards Plateau ecological region of

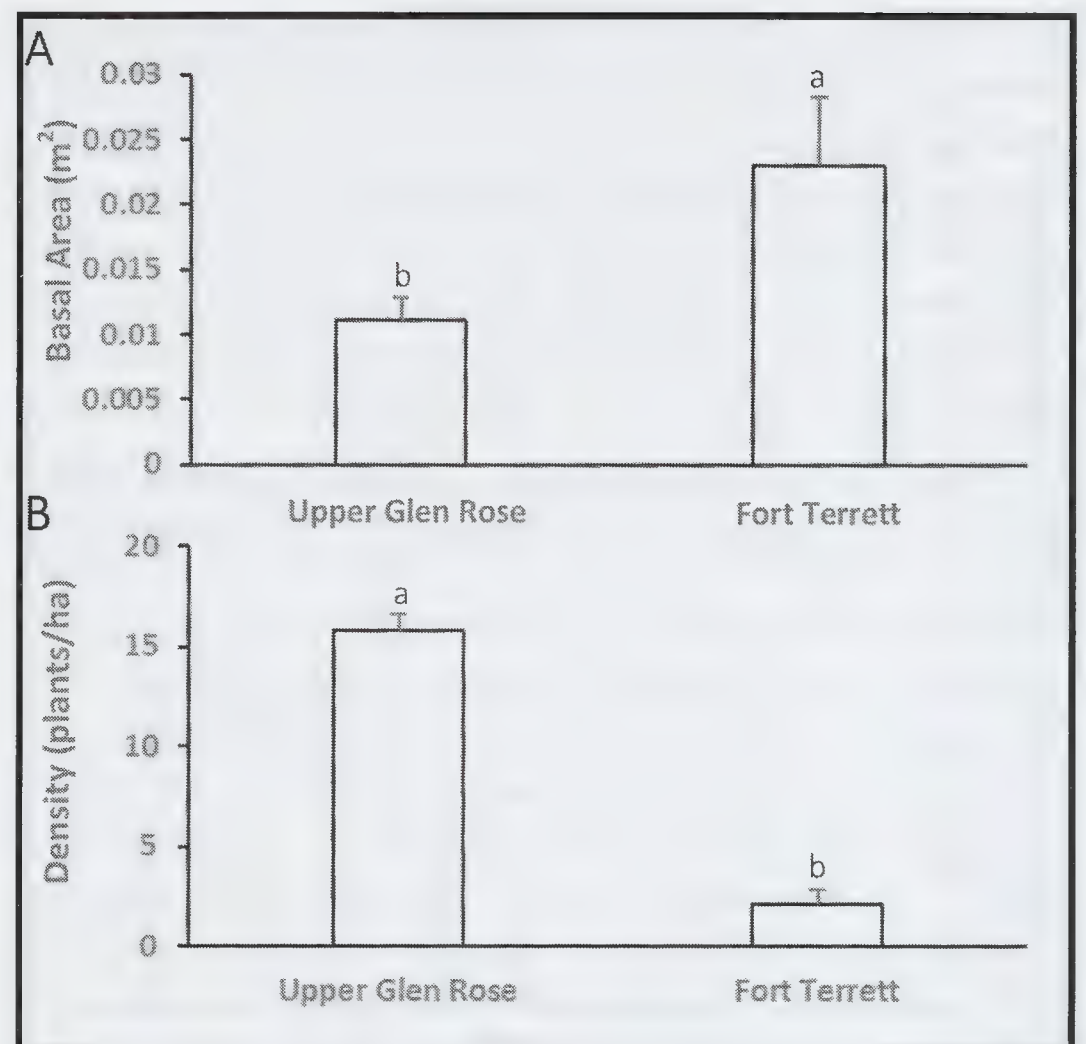


FIG. 5. Comparison of mean (± 1 SD) *Arbutus xalapensis* (A) basal area and (B) density by geologic substrate type. Sample size was 128. Means indicated with identical letters are not statistically different from one another ($\alpha = 0.05$).

Texas (Van Auken et al. 1979; Riskind and Diamond 1988; Van Auken 1988; Russell and Fowler 1999; Van Auken 2018). Many studies examining the vegetation composition of this region have been conducted, and though *Arbutus xalapensis* is known to occur in the region, it has yet to be reported in ecological studies and its community density and basal area have not been reported. Thus, where it specifically occurs has really not been thoroughly investigated (Van Auken et al. 1979; Van Auken 1988; Sorensen 1995; Van Auken et al. 2017; Van Auken 2018). *Arbutus xalapensis* is an evergreen tree that is known to have disjunct populations in Texas, and is found in various places in Mexico, and Central America (Amos and Rowell 1988; Tirmenstein 1990). Distribution of *A. xalapensis* is said to occur in canyon and creek bed habitats as well as on hillsides (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). This information, however, seems mostly anecdotal and vague. Almost all previous reports are notable for their lack of quantitative vegetation data, but attempt to place species, including *Arbutus xalapensis*, in an ecological framework based on plant occurrence and observation (Gehlbach 1967).

The present study examined three community types in which *A. xalapensis* has been observed within portions of central Texas. It was expected that *A. xalapensis* would be largest and have the highest density within the hillside communities. This did not occur. We found the largest *A. xalapensis* plants in the hilltop *Juniperus* communities. However, highest density of *A. xalapensis* was in the hillside communities. In the Guadalupe Mountains of west Texas and New Mexico, *A. xalapensis* has been reported in

canyons with *Acer grandidentatum* and *Quercus muehlenbergii* Engelm. as dominant species and *Juniperus deppeana* Steud., *Quercus grisea* Lieb., and *A. xalapensis* as important contributors to the nearly closed canopy (Gehlbach 1967). Also, in west Texas, *A. xalapensis* is widespread in the Davis Mountains, including wooded canyons, mountain slopes and drainages, but not specific habitats and no ecological characteristics are presented (Powell 1998). In southwest Arizona, the Arizona madrone (*Arbutus arizonica* Sarg.) is reported in *Quercus* woodlands (Epple and Epple 1995), in pine-oak woodlands and canyon bottoms in the pine-oak forest zone (Gehlbach 1981; Barton 2005; USDA NRCS 2016). The Pacific madrone (*A. menziesii* Pursh) is present from southwestern British Columbia into southern California, including the Sierra Nevada of central California (Whitney 1998). It is described from a number of habitats including foothills, upland slopes and canyons in oak and coniferous forests, where it is often in open forests, rocky slopes, ravines and also the understory. These reports make it difficult to predict where these species of madrone should be found in the environment, or if one or all madrone species are overstory or understory species.

Differences in geological substrates seemed to explain some of these dissimilarities, or differences at least, observed among the central Texas *A. xalapensis* populations. The Fort Terrett member of the Edwards limestone is a very hard limestone, with mostly shallow soils, and it occurs on hilltops in most of the ABK natural area and other areas in central Texas (Riskind and Diamond 1988; Woodruff et al. 1994). It appears that the *A. xalapensis* trees that we found on hilltops, on hard Edwards limestone established a long time ago because of their size. They are large trees and possibly established in limestone cracks where additional soil accumulated (Weaver and Jurena 2009). This is supported because mean soil depth where the trees were found was 16.0 cm, whereas general upland soils were 10.8 cm deep (Van Aukun et al. 2017). Soils of the Upper Glen Rose Formation were deeper, holding more water, and supporting a higher density of *A. xalapensis* trees (Van Aukun et al. 1981 and present study).

In several instances, results from the current study differed from existing reports (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). We found *A. xalapensis* populations in different habitats and with different ecological characteristics than some of the literature suggested (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012). Overall, basal area and height were both less than described in previous reports, which could be explained by collection site differences. In addition, the elevation range at which *A. xalapensis* was found in this study (493–589 m) was considerably lower than suggested in previous reports (1219–

3400 m) (Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015), but within the elevation range given in the Flora of North America (300–2200 m) (Sorensen 2009).

The density of *A. xalapensis* was highest in hillside communities, followed by canyon communities, where *A. xalapensis* was noted to occur, but *A. xalapensis* was also found in upland communities, where it was not reported previously (Riskind and Diamond 1988; Tirmenstein 1990; Gonzalez-Elizondo et al. 2012). The differences in the overall population size and distribution may not refute previous reports, but the results show that the central Texas populations are somewhat different than other populations previously described (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012). This may be possible because the area of study is different or more care was taken noting community or habitat type in the current study than in previous studies. Some of the parameters collected, especially height and basal area, may be used in the future to approximate the age of *A. xalapensis*, as has been done for other species (Ferguson and Carlson 2010).

Higher *A. xalapensis* density was found below a woodland canopy, where reduced light levels were previously recorded (Van Aukun et al. 2017). Lower light levels have been shown to be important in the growth and development of *A. xalapensis* juveniles, but higher light levels seem required for the growth and development of mature trees (suggested by Whitenberg and Hardesty 1978). *Juniperus ashei* and other *Juniperus* species seem to germinate, establish and grow best in low light conditions, while adults seem to require full sun (Van Aukun et al. 2004; McKinley and Van Aukun 2005; Kane et al. 2011). The same may be true for *A. xalapensis*.

Deepest soils were found within the canyon communities, but hillside soils were shallower than upland soils. Mean soil depth, within one meter of *A. xalapensis* individuals, within canyon and upland communities in the present study were deeper than the soil depth recorded within similar canyon and upland communities in a previous study (Van Aukun et al. 2017). Deeper soils may lead to increased retention of soil water and possibly other soil nutrients, and *A. xalapensis* establishing, growing, and surviving in deeper pockets of soil may be due to water-related stresses in associated shallower soil (Van Aukun et al. 1981; Weaver and Jurena 2009; Geroy et al. 2011). This would not seem to work in the canyon communities because of the lower light levels below the overstory canopy (Van Aukun et al. 2017).

This study showed that the central Texas populations of *A. xalapensis* are different than other populations previously described (Riskind and Diamond 1988; Tirmenstein 1990; Sorensen 1995; Mackay 1996; Gonzalez-Elizondo et al. 2012; Salas-Morales et al. 2015). Within the Edwards Plateau, *A.*

xalapensis appears to be shorter and with less girth than in other portions of its range. This may point to the already documented variability within the species or it may necessitate examining population genetics, competition, light requirements, or soil nutrient and water availability more carefully (Barbour et al. 1987). The analysis of density between habitats showed that *A. xalapensis* clearly favors lower slopes and does not readily establish in flat upland communities with shallow soils or canyon communities with deeper shade. More juvenile *A. xalapensis* plants than mature ones (not shown) suggest a potentially expanding population (Harper 1977; Barbour et al. 1987), which would be very interesting. It is also possible that *A. xalapensis* establishment only occurs sporadically or episodically.

We have barely scratched the surface concerning the ecology and distribution of *A. xalapensis* in south-central Texas. Other studies are needed to understand the ecological requirements of this species. These studies are necessary for prediction of future population structure of this species, especially demographic changes. In addition, how does the Texas *Arbutus* compare with the California, Arizona, Mexican and Central American madrones? No one knows the answer, but this information would be important for future conservation of these species.

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